Uncovering multiple influences on space use by deer mice using NEON data

Sean O'Fallon[1], Noa Pinter-Wollman[1], Karen Mabry[2]

1. Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, USA
2. Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

Corresponding author: Sean O'Fallon, seanofallon@g.ucla.edu, 618 Charles E Young Dr S, Los Angeles, CA 90095

Abstract

Space use by animals is affected by multiple factors; previous researchers have examined the effects of influences such as sex, body condition, and population density on home range area. However, evaluating the simultaneous influences of multiple factors on animal space use has been relatively intractable due to sample size limitations. We capitalize on National Ecological Observatory Network (NEON) data to ask what factors determine space use by deer mice (genus *Peromyscus*). We examined data from 10 years of repeated captures of individually identified mice at 36 sites across North America. We confirmed previous findings that males have larger home ranges than females and that home range area decreases with increasing animal density. In addition, our large sample size (N = 2420 individuals) enabled us to examine the interacting influences of these and other intrinsic and extrinsic factors using a robust statistical framework. We found that the relationship between body condition and home range area differs between male and female mice, and that habitat type, latitude, and animal density all interact to influence space use. We conclude that high throughput ecological data can be used to examine important behavioral questions that have long eluded investigators.

Keywords: Behavioral Ecology, Home range, NEON, Peromyscus, Space use, Utilization distribution

Introduction

A home range inhabited by an animal contains all of the resources that it needs for daily life; home range area (HRA) is the amount of space that an animal typically requires to meet its needs (Burt, 1943). Multiple factors, both internal (phenotypic) and external (environmental) to an animal, can influence HRA and these influences may reinforce or counteract each other. For example, an animal in good physical condition may be able to move over and utilize a larger area than an animal in poor condition. However, the effect of body condition on HRA may be offset by habitat quality: a more competitive animal that establishes its home range in a resource-rich environment can meet its daily needs in a smaller area. Given the potentially conflicting influences of multiple factors on HRA, it is important to examine the simultaneous effects of these factors on animal space use. Yet most studies of animal space use quantify HRA for one species in one place in relation to one or few factors that influence HRA, which makes it difficult to uncover synergies among factors that impact animal space use. Some researchers have dealt with the limitations of isolated home range studies through meta-analysis; for example, studies of metabolic scaling demonstrate that HRA scales with body size across species (Jetz et al., 2004; Kelt & Van Vuren, 2001; Ofstad et al., 2016). Further meta-analyses should be facilitated by the *HomeRange* database of home range estimates for almost 1,000 mammal species (Broekman et al., 2023).

Despite advances in large-scale meta-analyses of influences on HRA across taxa, simultaneous examination of multiple phenotypic and external factors on HRA in a single taxonomic group has remained challenging (Börger et al., 2006). Such analyses have been stymied by a suite of factors that limit the ability of researchers to simultaneously consider multiple influences on space use across large spatial and temporal scales. For example, methodological differences such as differences in the data types (i.e., live-trapping versus radio-tracking) or home range estimators (such as minimum convex polygon (MCP) versus kernel density estimators (KDEs)) used to determine HRA may obscure relationships between phenotypic and environmental predictors and HRA across the range of a species (Börger et al., 2006; Nilsen et al., 2008; Worton, 1989) and across different studies of the same species. Further, the most-often used methods for collecting the location data that are necessary to estimate HRA (live-trapping and radio-telemetry) have historically been both time- and labor-intensive (Kays et al., 2015; Wilmers et al., 2015). The logistical and financial challenges of carrying out such field studies have often limited individual researchers to working at a single site on small numbers of individuals, yielding information about HRA that can be difficult to synthesize with studies at other locations. The National Ecological Observatory Network (NEON), an NSF-funded long term project that collects and curates standardized biological data, opens up new opportunities to examine the synergistic influences of multiple phenotypic and environmental factors on animal home ranges (Dantzer et al., 2023).

Phenotypic attributes of individual animals, including sex, age, body condition, behavior, and neuroendocrine factors, are all expected to influence patterns of animal space use. Sex is likely the most-often tested effect of individual phenotypic variation on HRA in mammals (Clement & Roedder, 2021): male mammals often (but not always) have larger HRAs than female conspecifics (Stickel, 1968; Wolff, 1989). This difference in space use between males and females is typically attributed to one of two non-exclusive explanations: body size dimorphism and the promiscuous or polygynous mating systems of most mammalian species (Emlen & Oring, 1977; Wolff, 1989). Larger animals (typically males in mammalian species with sexual size dimorphism, but see (Tombak et al., 2023) often range over larger areas;

however, sexual size dimorphism has also been associated with non-monogamous mating systems (Andersson, 1994), and mating systems can influence space use (Clutton-Brock, 1989; Emlen & Oring, 1977). In polygynous mating systems, which are common in mammals (Waterman, 2007), males are expected to range over larger areas to find and access the home ranges of multiple females, while females are expected to use and defend smaller areas (which would then be considered territories; (Emlen & Oring, 1977)). The body condition of animals can also affect space use behavior, although it is more often evaluated in relation to dispersal than HRA (reviewed by Clobert et al., (2009)). In relation to dispersal, better body condition typically correlates with an increased likelihood to disperse (Holekamp, 1986), or increased dispersal distance. Body condition would be expected to influence HRA in a similar way: animals with good body condition should be able to use larger areas than animals in poor condition (Fokidis et al., 2007).

Environmental conditions, such as population density and habitat type, have also been found to affect space use behavior. Typically, population density is negatively correlated with HRA (Šálek et al., 2015; Schradin et al., 2010), and at increased population densities, animals may also exhibit increased home range overlap with neighbors and/or increased territoriality (Wolff, 1989)). For animals that use multiple types of habitat, HRA may vary with habitat type (e.g., Ofstad et al., 2016). However, it can be difficult to disentangle the effects of habitat type and population density on HRA, as these factors often covary (Stickel, 1968). Finally, for widely-distributed species, latitude (or factors associated with latitude, such as temperature and resource availability), may affect space use (Gonzalez-Borrajo et al., 2017; Mattisson et al., 2013; Morellet et al., 2013). For example, Gompper & Gittleman (1991) found that HRA of small carnivores increased with increasing latitude, likely because decreasing resource availability at higher latitudes necessitated the use of larger areas to obtain the resources needed to meet basic needs.

Here we leverage the power of the large temporal and spatial scale of data collected by the National Ecological Observatory Network (NEON) to simultaneously consider the influences of multiple phenotypic and environmental factors on HRA in the most abundant and widely-distributed genus of rodents in North America, *Peromyscus* (deer mice). NEON is a nation-wide network of field sites where a variety of ecological and organismal data are being collected over a 30-year period using standardized methodologies (Dantzer et al., 2023). NEON enables comparisons across large temporal and spatial scales; for example, examining the relationship between niche overlap and latitude in rodents (Read et al., 2018). NEON includes 47 terrestrial sites and small mammal live-trapping data are collected at the 44 of these sites (sites in Hawaii and Puerto Rico are excluded). The dataset that we use here includes captures from the 36 NEON sites with sufficient *Peromyscus* captures for the calculation of a home range, spanning almost 20 degrees of latitude and 10 years in three macrohabitat types (forest, grassland, and shrubland). We conducted our analyses at the genus, rather than species, level because the original NEON small mammal sampling protocol (Paull et al., 2023) predates a taxonomic revision of *P. maniculatus sensu lato*, which elevated multiple clades within *P. maniculatus sensu lato* to species status (Boria & Blois, 2023; Bradley & Lindsey, 2019; Greenbaum et al., 2019). Thus, all of these now-recognized species are coded as *P. maniculatus* in the NEON data set. Furthermore, morphological similarities between some distantly-related species lead to difficulty in reliably distinguishing some pairs of syntopic *Peromyscus* species in the field (e.g., *maniculatus*/*leucopus*, *maniculatus*/*keeni*, and *leucopus*/*gossypinus*). However, because most *Peromyscus* species are ecologically very similar and our predictions about space use are the same for all species included in our study, we condensed data to the genus level to avoid any impact that misclassification of species might have on our results. The remarkable spatial and temporal replication of the NEON dataset allows us to simultaneously investigate the roles of both phenotypic (sex and body condition) and environmental (density, habitat type, and latitude) factors, as well as interactions among these factors, on space use in *Peromyscus*. We predicted that males would have larger HRAs than females, that HRA would be negatively correlated with animal density but positively influenced by body condition, that HRA would increase with latitude, and that habitat type would affect HRA.

Materials and methods

NEON data

NEON collects small mammal capture data on 1 ha grids set with 100 Sherman traps at 10 x 10 meter intervals. Each terrestrial NEON site contains 3-8 small mammal trapping grids and each grid is sampled in 4-6 bouts each year, with bouts taking place over either 1 night (in the case of "diversity grids") or 3 nights (in the case of "pathogen grids"). When individuals from target species are captured, they are weighed, sexed, measured, and identified to genus, and when possible, to species, before being tagged with a unique identifier and released. Details on the NEON small mammal sampling protocol can be found at: https://data.neonscience.org/data-products/DP1.10072.001.

We retrieved all small mammal capture data available from NEON in January 2023 for use in our analysis. This initial dataset contained capture data on 169 species from 46 sites from 2013 to 2022. We filtered this initial dataset to include only captures of *Peromyscus*. We then removed records of *Peromyscus* species that exhibit some degree of social and/or genetic monogamy: *P. californicus*, *P. eremicus*, and *P. polionotus* (Dewsbury, 1981; Kalcounis-Rüppell & Ribble, 2007). Not only is monogamy an atypical mating system for the genus, monogamy would also be expected to influence predictions about sex differences in HRA (Emlen & Oring, 1977). These three species have relatively limited distributions and are morphologically easy to distinguish from other *Peromyscus* species (*P. californicus* and *P. polionotus* are the largest and smallest members of the genus, respectively). Thus, unlike some other species of *Peromyscus*, these three species can be reliably identified and removed from the dataset. After the removal of these three species, we were left with the following *Peromyscus* species in our dataset (ordered from largest to smallest sample size): *leucopus, maniculatus (sensu lato), gossypinus, boylii, truei*, *keeni*, and *attwateri*.

Home range area calculation

To calculate home range area, we computed the utilization distribution of each animal and considered the 50% kernel area as the HRA. We only included in this analysis animals that had five or more capture events at at least two unique locations. We used the functions kernelUD() and kernel.area() from the R package adehabitatHR (Calenge, 2006) to calculate 50% kernel density estimate home range areas.

We focused our analysis of HRA on animals that had five or more captures as adults based on a rarefaction analysis that determined that five locations provided sufficient information to obtain an accurate home range area using a utilization distribution (or kernel density estimation) approach (see supplementary materials). The rarefaction analysis further showed that using a minimum convex polygon (MCP) to calculate home range area was not a reliable method (as found by others: Socias-Martínez et al., 2023) and so we only used a utilization distribution (KDE) approach here to calculate HRA.

Assignment of sex

Although there are clear differences in external genitalia between male and female *Peromyscus*, misidentifications can occur, especially for non-reproductive animals. The sex of each individual in our analysis was assigned as the sex it was noted as in the NEON database for the majority of its capture events. For example, if an animal was noted as a male on more captures than it was noted to be a female, we considered it to be a male, and vice versa. We used 'pregnancy status' in the NEON database to further identify females. We considered any individual that was ever noted to be pregnant as a female, regardless of the number of times that it was noted as a male on other capture occasions. If pregnancy was never observed and the number of times an animal was noted as male was equal to the number of times it was noted to be a female, we designated its sex as 'unknown'.

Determining animal age

We included only captures of adult animals in our analysis because space use by juveniles may reflect use of the mother's home range, dispersal, or other developmental processes that do not reflect typical space use for an individual. Thus, if an animal was captured when it was both a juvenile and an adult, we considered in our analysis only its captures as an adult. Each capture was assigned a lifestage in the field, but we assigned a lifestage to each capture based on body mass to avoid relying on subjective criteria such as stage of the post-juvenal molt, which may be applied unevenly across observers.

We applied body mass cut-offs based on existing body mass data in relation to developmental stage for each species in our dataset, grouping species into ‘small’ and ‘large’ categories (Derrickson, 1988; Drickamer & Bernstein, 1972; Layne, 1968; McCabe & Blanchard, 1950; Pournelle, 1952; Wolff et al., 1988). Mass records differed significantly between these two categories (p-value < 0.001; see Figure S2A), justifying our assignment of each species. For ‘small’ species (*maniculatus*, *leucopus*), we assigned ‘subadult’ lifestage to captures < 16 g and ‘adult’ lifestage to captures 16+ g. For ‘large’ species (all others: *keeni*, *truei*, *gossypinus*, *attwateri*, and *boylii*), we assigned ‘subadult’ lifestage to captures < 19 g and ‘adult’ lifestage to captures 19+ g. In some cases, individuals were assigned as adults based on body mass at an early capture, but later it lost mass, dropping below the adult mass cut-off, or its mass was not recorded. To account for this weight loss and missing data, we assigned ‘adult’ lifestage to all captures of an individual that occurred after the first time it was above the ‘adult’ threshold.

Computing body condition

To determine the body condition of each individual, we calculated the mean body mass (g) and mean hindfoot length (mm) for each mouse from all of its captures (Schulte-Hostedde et al., 2005). To avoid the confounding effects of pregnancy on body condition estimates, we excluded from this calculation any captures when an individual was pregnant or when pregnancy status was listed as ‘unknown’. We then regressed the mean mass against the mean hindfoot length using the lm() function in R ‘base’, and assigned the residuals of this regression to each individual in our dataset as their body condition. We conducted these regressions and body condition assignment separately for the ‘small’ and ‘large’ species to account for differences in mass and hindfoot length between large and small species (Figure S2B,C).

Vegetation types

To examine the effect of vegetation type on home range area, we grouped NEON’s ‘vegetation types’ into three categories to ease analysis and biological interpretation. The three categories were: forest (NEON vegetation types 'deciduousForest', 'mixedForest', 'evergreenForest', and 'woodyWetlands'), grassland (NEON vegetation types 'grasslandHerbaceous', 'cultivatedCrops', and ‘pastureHay’) and shrubland (NEON vegetation type 'shrubScrub').

Calculating animal density

To determine the density of *Peromyscus* that each focal individual experienced, we calculated the minimum number of *Peromyscus* individuals known alive (MNKA) at each plot on each sampling date. For this calculation, individuals were considered to be “known alive” for all sampling dates between their first and last captures at the sampling plot. We assigned each individual in our dataset an ‘average MNKA’ which was the mean of all MNKA values for the plot in which the focal individual was captured during all sampling dates between the first and last capture of the focal individual.

Removing outliers

Some of the capture records had weight above 50 g (N=8, out of 23,959) or hindfoot length greater than 28 mm (N=7, out of 23,959). These values are unlikely for the species in our dataset, therefore we replaced the values for weight and hindfoot length with NA for those 15 records and included them only for the home range analysis (but not the body condition analysis). We also removed one individual (out of 2,420) that was recorded as 9g, which is an unrealistically low weight for an adult. In addition, we removed one individual with inconsistent pregnancy status (i.e., consecutive days fluctuating between positive and negative pregnancy status).

Statistical analysis

To determine what factors impact HRA in *Peromyscus*, we used a statistical model selection approach in which we compared Generalized Mixed Models (GLMMs) with different interaction terms between the factors of interest (see Supplementary Materials for a list of the models tested and their comparison). We only included interaction terms that had biological meaning (Johnson & Omland, 2004). In all models, HRA was the response variable. Explanatory variables included sex, body condition, vegetation type, animal density (meanMNKA), and latitude as fixed effects. All models also included year and site as random effects to account for variation across years and sites in the model. All models were fitted with a Gamma log link function using the ‘lme4’ R package (Bates et al., 2015) and analysis of deviance tables were obtained using the Anova() function in the ‘car’ R package (Fox & Weisberg, 2019). We examined if models met all statistical assumptions (like linearity, homogeneity of variance, etc) using the check_model() function in the package ‘performance’ {ref}. Finally, we compared the AIC values of all models examined using the compare_performance() function in the package ‘performance’ (Lüdecke et al., 2021). We selected the best fit model based on AIC weight.

Results

Of the 12 models we tested, the best fit model included interaction terms between sex and body condition, habitat type and latitude, latitude and animal density, habitat type and animal density, and habitat type, animal density, and latitude (three-way interaction) (AIC weight = 0.98, Table 1, for all AIC values see Table S1). The main factors that had a significant impact on home range area were sex, habitat type, latitude, and animal density (Table 1). Interestingly, body condition by itself did not have a significant impact on home range area, it only impacted home range area when considering its interaction with sex. Overall, males had larger home ranges than females (Figure 1) and as male body condition improved, HRA increased (Figure 2). In contrast, as female body condition improved, HRA decreased (Figure 2).

Home range area varied by habitat type, with the smallest areas used in forested habitat and the largest in grasslands. Home range areas in shrublands were intermediate and not significantly different from home range areas in forests and grasslands (Post hoc Tukey test, Figure 3).

Home range area increased with latitude (Figure 4) and decreased with animal density (Figure 5). There was a significant interaction between latitude and animal density, which means that the effect of animal density on HRA differs across latitudes. While latitude and animal density are positively correlated with one another (Figure S3), suggesting that latitude might explain animal density rather than HRA, the fact that the relationship between HRA and latitude is in the opposite direction of the relationship between HRA and animal density, indicates that both factors have an important impact on home range area, regardless of the impact of latitude on animal density.

Finally, we found a significant interaction between latitude, animal density, and habitat type, which means that the relationship between HRA, latitude, and animal density differs across habitat types. Indeed, in forests, home range areas are larger at higher latitudes, and the decline in HRA with increasing animal density is slightly more steep in low latitudes than in high latitudes (Figure 6A). In contrast, home range areas in shrublands are larger at lower latitudes than at higher latitudes. The decline of HRA with animal density in shrublands does not seem to differ across latitudes, but the rate of this decrease (slope of the line) is smaller than in forests (Figure 6B). Finally, in grasslands, home range areas are larger in high compared to low latitudes when animal density is low, but as animal density increases, home range areas decrease as latitude increases. Thus, the rate at which home range areas decrease with animal density (slope of the line) is greater in high latitudes than in low latitudes in grassland habitats (Figure 6C).

Table 1: Analysis of deviance of the best fit model.

Effect	**Chisq**	**Df**	**P-value**
Sex	**138.188**	**1**	**< 0.0001**
Body Condition	1.059	1	0.303
Habitat type	**6.657**	**2**	**0.036**
Latitude	**9.257**	**1**	**0.002**
Animal density (meanMNKA)	**286.201**	**1**	**< 0.0001**
Sex x Body Condition	**10.287**	**1**	**0.001**
Habitat type x Latitude	5.840	2	0.054
Latitude x Animal density (meanMNKA)	**14.731**	**1**	**0.0001**
Habitat type x Animal density (meanMNKA)	5.859	2	0.053
Latitude x Habitat type x Animal density	**19.242**	**2**	**<0.0001**

(meanMNKA)			

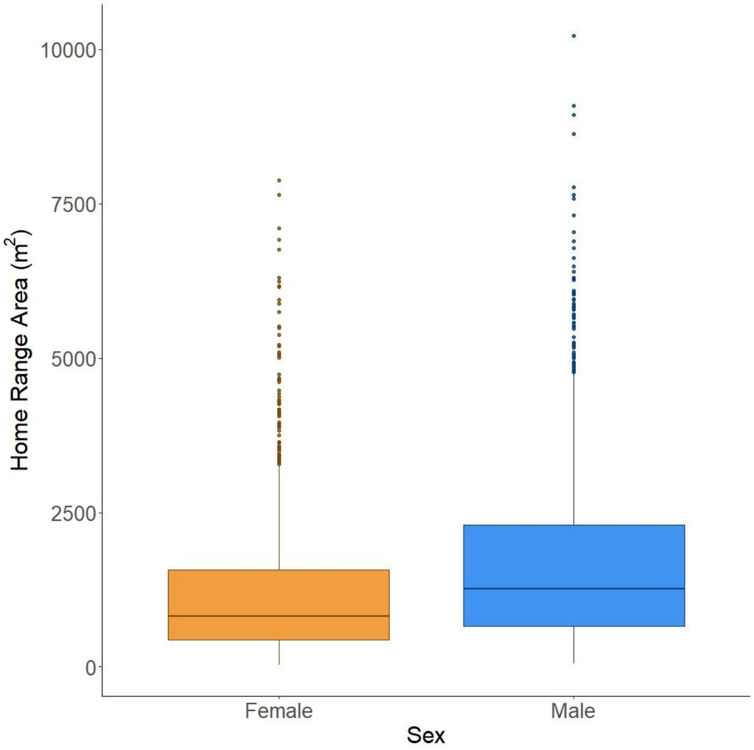


Figure 1. Home range area (m^2) by sex - males in blue and females in orange. Horizontal lines indicate the median, boxplots indicate the interquartile range, vertical lines extend to 1.5 times the interquartile range, and points indicate outliers.

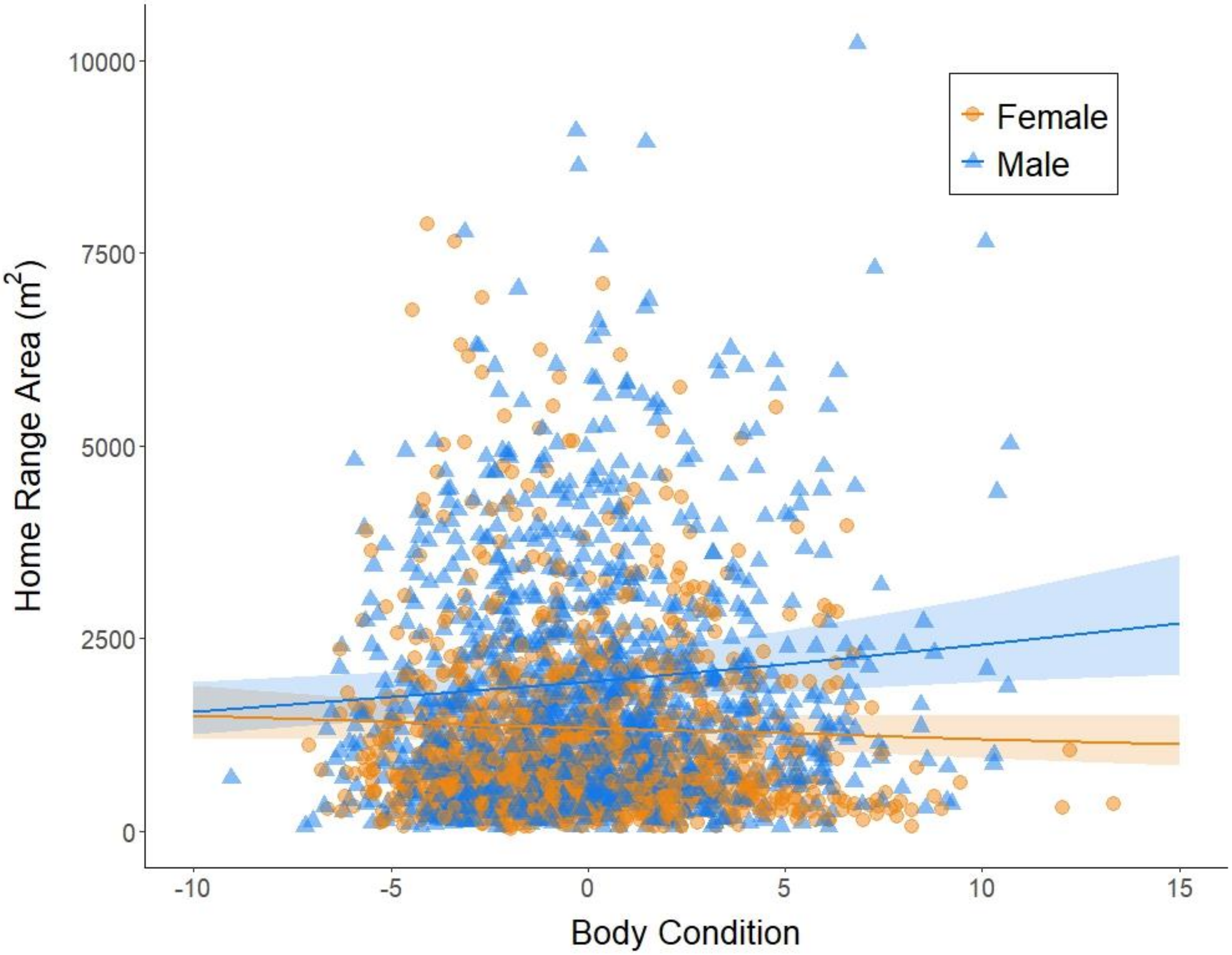


Figure 2. Home range area (m^2) as a function of body condition for males (blue triangles) and females (orange circles). Each point is an individual mouse and the lines are the predicted values from the statistical model, with confidence intervals as shaded areas around the lines.

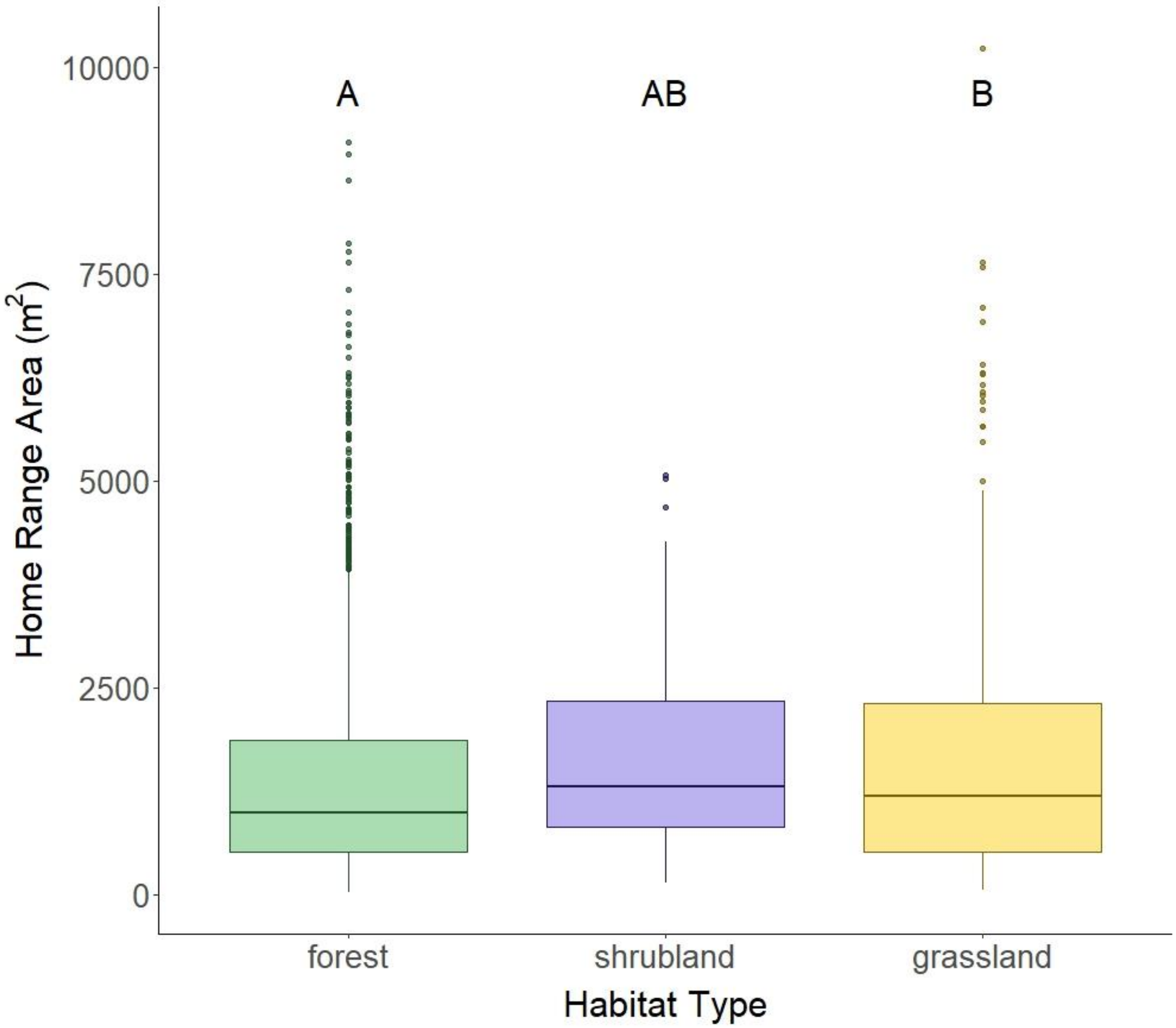


Figure 3: Home range area (m^2) by habitat type - forests in green, shrublands in purple, and grasslands in yellow. Horizontal lines indicate the median, boxplots indicate the interquartile range, vertical lines extend to 1.5 times the interquartile range, and points indicate outliers. Boxes that do not share a letter above them are statistically significantly different according to a post hoc Tukey test.

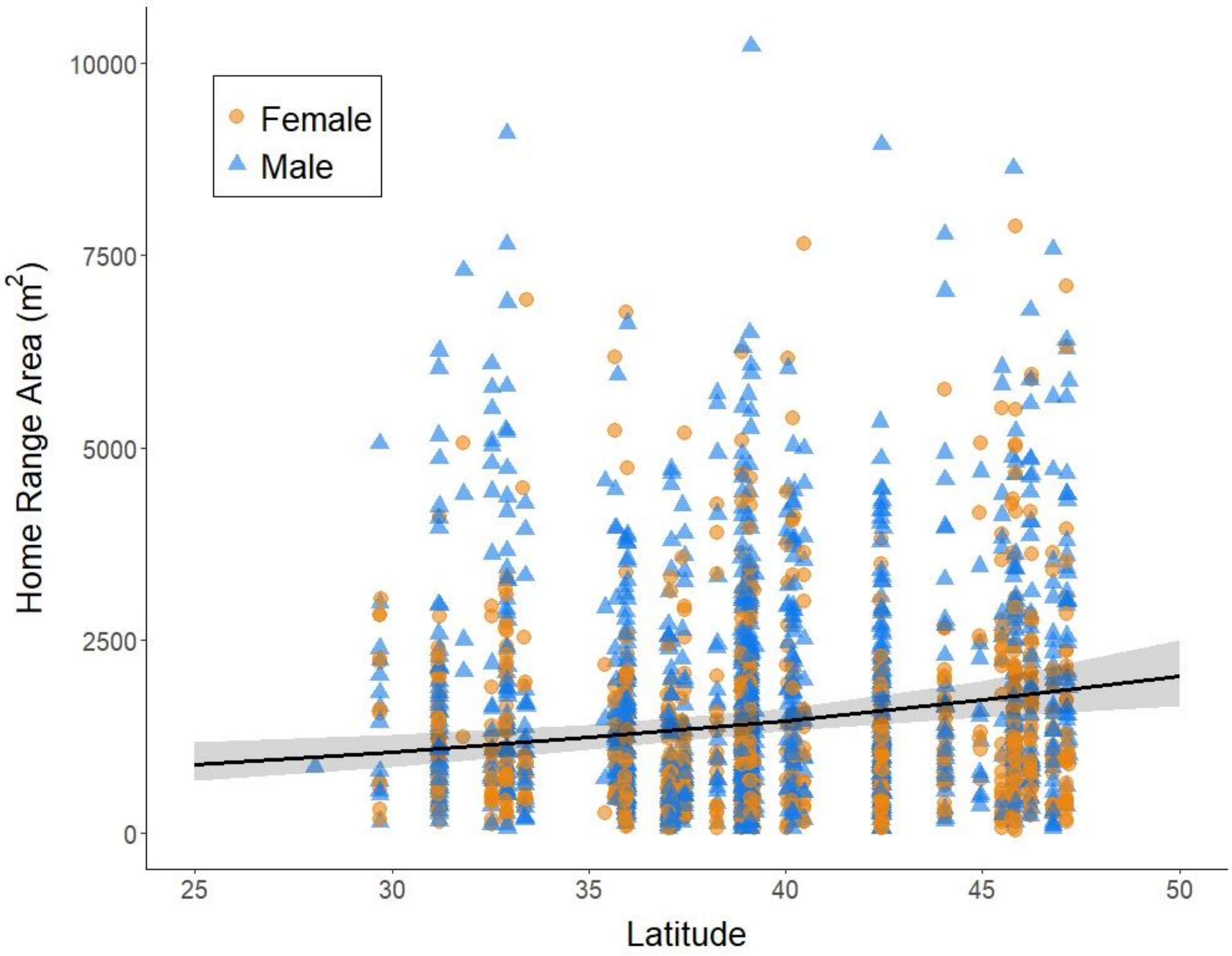


Figure 4. Home range area (m^2) as a function of latitude for males (blue triangles) and females (orange circles). Each point is an individual mouse and the line is the predicted values from the statistical model, with confidence intervals as shaded areas around the line.

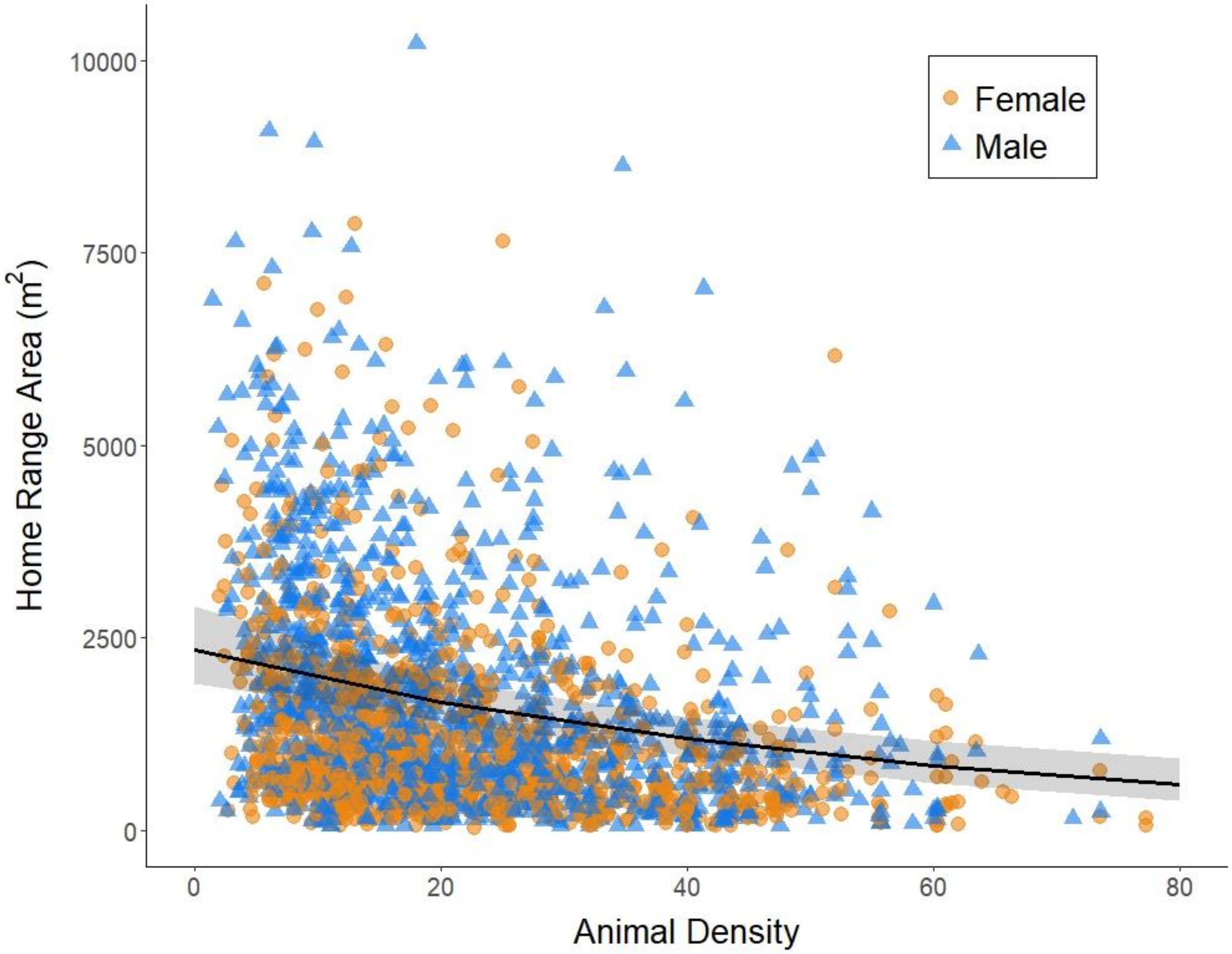


Figure 5. Home range area (m^2) as a function of animal density for males (blue triangles) and females (orange circles). Each point is an individual mouse and the line is the predicted values from the statistical model, with confidence intervals as shaded areas around the line.

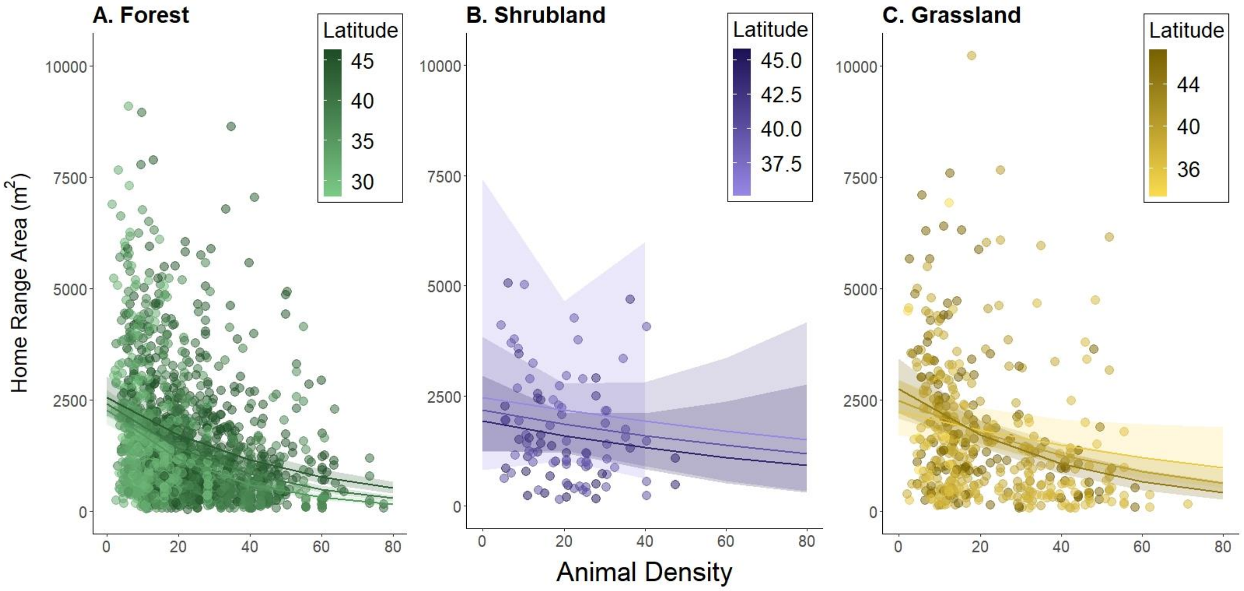


Figure 6. Home range area (m^2) as a function of animal density in (A) forests (green), (B) shrublands (purple), and (C) grasslands (yellow). Each point is an individual mouse and darker points are from higher latitudes (see color scale in each panel). The lines show relationships for three latitude ranges, determined by the emmeans() function. Note that the statistical model treats latitude as a continuous variable but three discrete lines are shown to assist the interpretation of the statistical interaction between animal density, latitude, and habitat type.

Discussion

Despite long-standing interest in the simultaneous effects of phenotypic and environmental conditions on space use by animals, such studies have been hampered by both small sample sizes and methodological differences across studies. Here, we leveraged the power of replication across time and space by the National Ecological Observatory Network (NEON) to investigate multiple simultaneous influences on space use by *Peromyscus* mice, analyzing the home range areas of almost 2,500 animals trapped across 10 years and almost 20 degrees of latitude. Our analyses confirmed generally accepted effects of sex and density on HRA: male mice had larger HRAs than did females (Figure 1), and HRA declined with increasing density of congeners (Figure 5).

However, the novelty of this study lies in our ability to detect interactive effects on space use, due to the large sample size and temporal and spatial replication provided by NEON. Because NEON employs consistent sampling methodologies across sites, we can be confident that observed differences across latitudes and habitat types are not mere artifacts of variation in sampling methods across studies and researchers. Importantly, the large sample size also gives us the necessary statistical power to conduct robust statistical tests that include interaction effects, and the top-ranked model in our analysis included statistically significant effects of both phenotypic (sex*body condition) and environmental (latitude*habitat type*animal density) effects on space use (Table 1).

It is not surprising that we found that on average, male *Peromyscus* have larger HRAs than do females (Figure 1). However, the interaction between sex and body condition reveals additional nuance: as body condition increases, male mice use larger home ranges whereas female mice use smaller home ranges (Figure 2). This result is consistent with established theory about space use by male and female mammals: Emlen and Oring (1977) posited that the distribution of female mammals across a landscape should be influenced by the distribution of resources, and the distribution of males should be influenced by the locations of females. Under Emlen and Oring's theory, the male strategy for maximizing reproductive success is to overlap more female home ranges and sire offspring by as many females as possible, while the female strategy is to obtain the resources needed to produce their offspring as efficiently as possible. This classic theory of differential space use by the sexes is almost certainly too simplistic (for example, multiple mating by both sexes is now known to be common across mammals), but our results are consistent with expectations arising from it: as body condition increases, male *Peromyscus* range more widely (Figure 2). Meanwhile, our results suggest that females with higher body condition do not need as much space to meet their energetic needs, due either to their internal energetic reserves, or because they are stronger competitors for better quality habitat where they can obtain sufficient energy over a smaller area. Importantly, we removed from our analysis any females who were pregnant, so the higher values of female body condition do not reflect temporary mass gains (and inflated body condition scores) due to pregnancy.

Environmental factors, including habitat type, animal density, and latitude all had important effects on home range area. We found that HRA was smallest in structurally more complex forested habitat types and largest in grassland habitat types, with intermediate HRAs in shrubland habitat (Figure 3). *Peromyscus* often utilize vertical habitat structure such as trees and shrubs, meaning that mice in more complex habitat types, where animals can use vertical space and thus have large 3D volumes of home range (like forests), may well have smaller 2D HRA estimates when considering space use in only one plane. Use of arboreal habitat may influence estimates of home range size, although the role of vertical habitat structure is rarely considered when estimating space use (Marines-Macías et al., 2018; Rader & Krockenberger, 2006). While this effect of habitat type on HRA seems straightforward, such analyses are rare due to the difficulty of conducting the necessary field work across larger spatial scales while also controlling for potential differences in animal density across space and habitat types.

When examining the effect of animal density on HRA, we replicated the known relationship between the density of competitors (including both conspecifics and congeners) and HRA: as density increases, HRA decreases (Figure 5). However, the increased model complexity in our study, enabled by the use of NEON data, revealed a more complicated picture for the effects of environmental conditions on HRA: while HRA declines with increasing mouse density for all combinations of latitude and habitat, the intercept of this relationship varies. Specifically, the intercept of the relationship between density and HRA is reversed between forest and shrub habitat types (Figure 6). In forested habitats, larger HRAs are found at higher latitudes (Figure 6A); the reverse pattern is seen in shrub habitats, where HRAs are smaller at higher latitudes (Figure 6B). Meanwhile, the slope of the relationship between density and HRA varies with latitude in grassland habitat (Figure 6). In grassland habitats, HRA declines more steeply with increasing mouse density at higher latitudes (Figure 6C); that is, density has a bigger impact on HRA as latitude increases. One potential explanation for this interaction between animal density, latitude and habitat type is that we collapsed multiple species of *Peromyscus* into a single analysis, as species may differ in the range limits of and habitat types they use. However, 80% of the individuals included in our study were field-identified as either *Peromyscus maniculatus (sensu lato)* or *P. leucopus*. Not only are these species found across the entire range of latitudes in our study (Table S2), these species are known to use multiple types of habitat. *P. maniculatus sensu lato* is the quintessential example of a habitat generalist mammal, with recognized ecomorphs (forest and prairie deer mice) that occur syntopically (Dice, 1922; Wecker, 1963). Thus, while recognizing potential issues with combining multiple species into a single analysis, the majority of individuals in our data set are from species that are both widely distributed (Table S2) and found across multiple habitat types.

Our work shows that high throughput ecological data can be used to reveal important behavioral questions that have long eluded investigators. With a large sample size that spans the continent spatially and an entire decade temporally, we were able to uncover novel relationships between animal space use and both phenotypic and environmental factors. Thus, large ecological monitoring networks can be used not only to uncover changes in ecological patterns, but also to examine how organismal biology will change as our world continues to be impacted by human activities.

Acknowledgments

We thank Kaija Gahm, Alejandra Gamboa, and Elvira Bastiani for helpful feedback on this work. This project emerged from a workshop as part of the “Integrating Organismal Biology into NEON” RCN organized by Ben Dantzer, Lynn Martin II, and KEM. The National Ecological Observatory Network is a program sponsored by the National Science Foundation and operated under cooperative agreement by Battelle. This material is based in part upon work supported by the National Science Foundation through the NEON Program.

Funding Statement

This work was supported by NSF MCA 2120988 to KEM. The “Integrating Organismal Biology into NEON” RCN is supported by NSF RCN 2110233 to Ben Dantzer, Lynn Martin II, and KEM.

Conflict of Interest

The authors have no conflict of interest to declare.

Author Contribution statement

All authors contributed to the conceptualization of the study questions and design, KEM provided expertise on the study organism, SO and NPW wrote code for data analysis, SO produced data visualization, all authors contributed to interpreting the results and writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study utilizes open access data collected across North America, where all authors are based.

Data accessibility

All data (downloaded from the NEON repository) and analysis code are available on Github: https://github.com/seanofallon/neon-mice_home-ranges.

References

Andersson, M. (1994). *Sexual selection* (Vol. 72). Princeton University Press.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, *75*(6), 1393–1405.

Boria, R. A., & Blois, J. L. (2023). Phylogeography within the *Peromyscus maniculatus* species group: Understanding past distribution of genetic diversity and areas of refugia in western North America. *Molecular Phylogenetics and Evolution*, *180*, 107701. https://doi.org/10.1016/j.ympev.2023.107701

Bradley, R., & Lindsey, L. (2019). Mitochondrial DNA sequence data indicate evidence for multiple species within *Peromyscus maniculatus*. *Special Publications, Museum of Texas*

Tech University.

Broekman, M. J. E., Hoeks, S., Freriks, R., Langendoen, M. M., Runge, K. M., Savenco, E., ter Harmsel, R., Huijbregts, M. A. J., & Tucker, M. A. (2023). HomeRange: A global database of mammalian home ranges. *Global Ecology and Biogeography*, *32*(2), 198–205. https://doi.org/10.1111/geb.13625

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*(3), 346–352. https://doi.org/10.2307/1374834

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Clement, V. F., & Roedder, D. (2021). Playing favourites-a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. *North-Western Journal of Zoology*, *17*(1).

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, *12*(3), 197–209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Clutton-Brock, T. H. (1989). Review lecture: Mammalian mating systems. *Proceedings of the Royal Society of London. B. Biological Sciences*, *236*(1285), 339–372.

Dantzer, B., Mabry, K. E., Bernhardt, J. R., Cox, R. M., Francis, C. D., Ghalambor, C. K., Hoke, K. L., Jha, S., Ketterson, E., & Levis, N. A. (2023). Understanding organisms using ecological observatory networks. *Integrative Organismal Biology*, *5*(1), obad036. https://doi.org/10.1093/iob/obad036

Derrickson, E. M. (1988). Patterns of postnatal growth in a laboratory colony of *Peromyscus leucopus*. *Journal of Mammalogy*, *69*(1), 57–66. https://doi.org/10.2307/1381747

Dewsbury, D. A. (1981). An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents. *Biologist*, *63*(4), 138–162.

Dice, L. R. (1922). Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. *Ecology*, *3*(1), 29–47. https://doi.org/10.2307/1929088

Drickamer, L. C., & Bernstein, J. (1972). Growth in two subspecies of *Peromyscus maniculatus*. *Journal of Mammalogy*, *53*(1), 228–231. https://doi.org/10.2307/1378859

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223. https://doi.org/10.1126/science.327542

Fokidis, H. B., Risch, T. S., & Glenn, T. C. (2007). Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, *73*(3), 479–488. https://doi.org/10.1016/j.anbehav.2006.08.010

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (Third). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gompper, M. E., & Gittleman, J. L. (1991). Home range scaling: Intraspecific and comparative trends. *Oecologia*, *87*(3), 343–348. https://doi.org/10.1007/BF00634589

Gonzalez-Borrajo, N., López-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas, and ocelots: A review of the state of knowledge. *Mammal Review*, *47*(1), 62–75. https://doi.org/10.1111/mam.12081

Greenbaum, I. F., Honeycutt, R. L., & Chirhart, S. E. (2019). Taxonomy and phylogenetics of the *Peromyscus maniculatus* species group. *From Field to Laboratory: A Memorial Volume in Honor to Robert J. Baker*, *71*, 559–575.

Holekamp, K. E. (1986). Proximal causes of natal dispersal in Belding's Ground Squirrels (*Spermophilus Beldingi*). *Ecological Monographs*, *56*(4), 365–391. https://doi.org/10.2307/1942552

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. *Science*, *306*(5694), 266–268. https://doi.org/10.1126/science.1102138

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, *19*(2), 101–108. https://doi.org/10.1016/j.tree.2003.10.013

Kalcounis-Rüppell, M. C., & Ribble, D. O. (2007). *A phylogenetic analysis of the breeding systems of Neotomine-Peromyscine rodents* (J. O. Wolff & P. W. Sherman, Eds.). University of Chicago Press Chicago, Illinois.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kelt, D. A., & Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist*, *157*(6), 637–645. https://doi.org/10.1086/320621

Layne, J. N. (1968). Ontogeny. In J. A. King (Ed.), *The biology of* peromyscus *(Rodentia)* (pp. 148–253). Spec Publ Am Soc Mammal.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Marines-Macías, T., Colunga-Salas, P., Verde Arregoitia, L. D., Naranjo, E. J., & León-Paniagua, L. (2018). Space use by two arboreal rodent species in a Neotropical cloud forest. *Journal of Natural History*, *52*(21–22), 1417–1431. https://doi.org/10.1080/00222933.2018.1459921

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J. D., Rauset, G. R., & Pedersen, H. C. (2013). Home range size variation in a recovering wolf population: Evaluating the effect of environmental, demographic, and social factors. *Oecologia*, *173*, 813–825. https://doi.org/10.1007/s00442-013-2668-x

McCabe, T. T., & Blanchard, B. D. (1950). *Three species of Peromyscus*. Rood Associates. https://cir.nii.ac.jp/crid/1130000797677126016

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J. D. C., Nicoloso, S., Sustr, P., Urbano, F., & Mysterud, A. (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*(6), 1326–1339. https://doi.org/10.1111/1365-2656.12105

NEON (National Ecological Observatory Network). Small mammal box trapping (DP1.10072.001), provisional data. **Dataset accessed from https://data.neonscience.org/data-products/DP1.10072.001.**

NEON (National Ecological Observatory Network). Small mammal box trapping (DP1.10072.001), RELEASE-2023. **https://doi.org/10.48443/p4re-p954.**

Nilsen, E. B., Pedersen, S., & Linnell, J. D. C. (2008). Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecological Research*, *23*(3), 635–639. https://doi.org/10.1007/s11284-007-0421-9

Ofstad, E. G., Herfindal, I., Solberg, E. J., & Sæther, B.-E. (2016). Home ranges, habitat and body mass: Simple correlates of home range size in ungulates. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1845), 20161234. https://doi.org/10.1098/rspb.2016.1234

Paull, S. (2022). Data tutorial: Introduction to Small Mammal Data. NEON (National Ecological Observatory Network). **https://www.neonscience.org/resources/learning-hub/tutorials/mammal-data-intro**

Paull, S., Thibault, K.M., Tsao, K., Springer, Y., Knapp, L. (2023). TOS protocol and procedure: mam – small mammal sampling. NEON.DOC.000481vO. NEON (National Ecological Observatory Network).

Pournelle, G. H. (1952). Reproduction and early post-natal development of the cotton mouse, *Peromyscus gossypinus gossypinus*. *Journal of Mammalogy*, *33*(1), 1–20. https://doi.org/10.2307/1375637

Rader, R., & Krockenberger, A. (2006). Three-dimensional use of space by a tropical rainforest rodent, *Melomys cervinipes*, and its implications for foraging and home-range size. *Wildlife Research*, *33*(7), 577–582. https://doi.org/10.1071/WR04117

Read, Q. D., Grady, J. M., Zarnetske, P. L., Record, S., Baiser, B., Belmaker, J., Tuanmu, M.-N., Strecker, A., Beaudrot, L., & Thibault, K. M. (2018). Among-species overlap in rodent body size distributions predicts species richness along a temperature gradient. *Ecography*, *41*(10), 1718–1727. https://doi.org/10.1111/ecog.03641

Šálek, M., Drahníková, L., & Tkadlec, E. (2015). Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review*, *45*(1), 1–14. https://doi.org/10.1111/mam.12027

Schradin, C., Schmohl, G., Rödel, H. G., Schoepf, I., Treffler, S. M., Brenner, J., Bleeker, M., Schubert, M., König, B., & Pillay, N. (2010). Female home range size is regulated by resource distribution and intraspecific competition: A long-term field study. *Animal Behaviour*, *79*(1), 195–203. https://doi.org/10.1016/j.anbehav.2009.10.027

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of mass–size residuals: Validating body condition indices. *Ecology*, *86*(1), 155–163. https://doi.org/10.1890/04-0232

Socias-Martínez, L., Peckre, L. R., & Noonan, M. J. (2023). Are trapping data suited for home-range estimation? *Ecography*, *2023*(3), e06442. https://doi.org/10.1111/ecog.06442

Stickel, L. F. (1968). Home range and travels. In J. A. King (Ed.), *The biology of* peromyscus *(Rodentia)* (Vol. 2, pp. 373–411). Spec Publ Am Soc Mammal.

Tombak, K. J., Hex, S. B. S. W., & Rubenstein, D. I. (2023). *New estimates indicate that males are not larger than females in most mammals* (p. 2023.02.23.529628). bioRxiv. https://doi.org/10.1101/2023.02.23.529628

Waterman, J. (2007). Male mating strategies in rodents. In J. O. Wolff & P. W. Sherman (Eds.), *Rodent Societies: An Ecological and Evolutionary Perspective* (pp. 27–41). University of Chicago Press.

Wecker, S. C. (1963). The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecological Monographs*, *33*(4), 307–325. https://doi.org/10.2307/1950749

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741–1753. https://doi.org/10.1890/14-1401.1

Wolff, J. O. (1989). Social behavior. In G. L. Kirkland Jr. & J. N. Layne (Eds.), *Advances in the Study of Peromyscus (Rodentia)* (pp. 271–291). Texas Tech University Press, Lubbock.

Wolff, J. O., Lundy, K. I., & Baccus, R. (1988). Dispersal, inbreeding avoidance and reproductive success in white-footed mice. *Animal Behaviour*, *36*(2), 456–465.

https://doi.org/10.1016/S0003-3472(88)80016-2

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*(1), 164–168. https://doi.org/10.2307/1938423

<u>Supplementary Materials for:</u>

Uncovering multiple influences on space use by deer mice using NEON data

Table of contents:

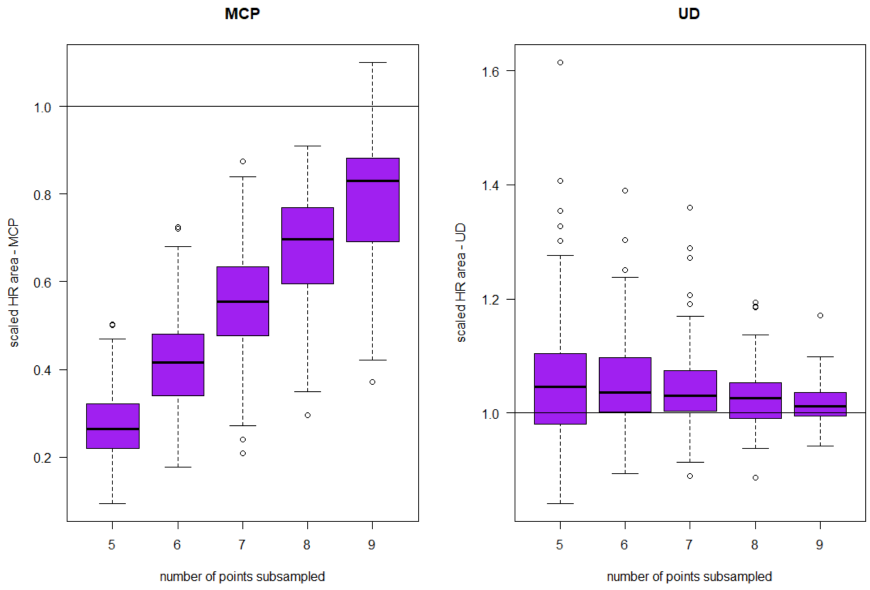
---

1. Rarefaction of home range

Number of captures used to estimate home range:

To determine the smallest number of captures that could be used to obtain a reliable estimate of home range size, we ran a sub-sampling analysis. In this analysis we only used individuals that had 10 or more captures (N=93) and the largest number of captures was 25. We calculated an ‘observed’ home range size using all available capture information for each individual with either a minimum convex polygon (MCP) or a utilization distribution (UD) using the functions mcp.area() and kernel.area() in the R package ‘adehabitatHR’ {ref}. We then sub-sampled (without replacement) the captures of each individual to take 5,6,7,8,or 9 random captures from those available for each individual. We sampled each individual and each sample size 50 times and calculated home range sizes using the sub-sampled data with both MCP and UD home range estimates. We scaled each home range obtained from the sub-sampled data to the ‘observed’ home range (which was calculated using all available data points for each individual) by dividing the sub-sampled home range by the observed home range. A scaled home range value equal to 1 means that the home range from the sub-sampled data is identical to the home range calculated from all samples available for the individual. Values smaller than 1 indicate that the sub-sampled data underestimates home range size and values larger than 1 indicate that the sub-sampled data overestimates the observed home range size. To examine the impact of number of data points (captures) on our ability to estimate an individual's home range, we averaged the scaled home range (MCP or UD) for each individual over the 50 runs of the simulation for each number of subsampled captures (i.e., 5,6,7,8,and 9). We thus obtained 93 values of scaled home range sizes for each sample size we examined (5-9) for both MCP and UD home range estimates (Figure S1).

Figure S1: Scaled home range sizes from the sub-sampling analysis using MCP (left) or UD (right) estimates for home range. We compared 5 different sample sizes (5-9) depicted on the x axis. Each individual was sub-sampled 50 times for each sample size and the scaled home range sizes for each individual was averaged over the 50 simulation runs. Boxplots show the averaged scaled home ranges for each sample size for the 93 individuals we used in this analysis.



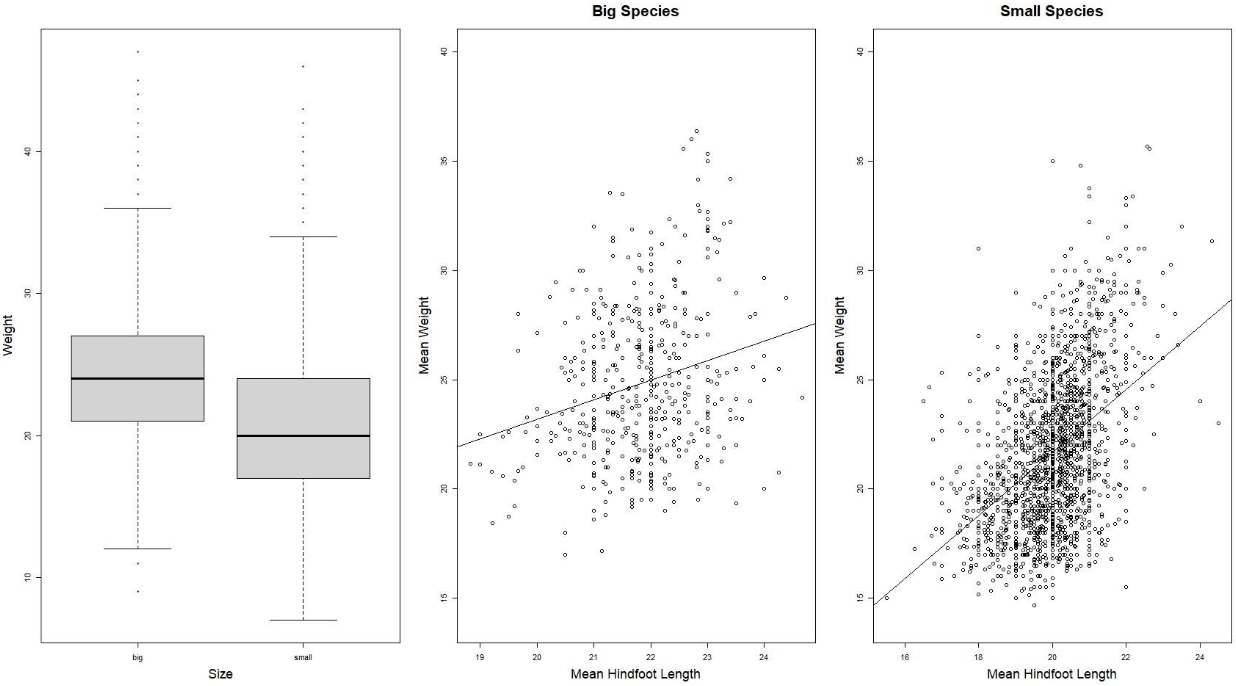
Results: We found that when using an MCP estimate, as the number of data points (captures) increased we obtained home range size estimates that were closer to those observed when using all available data points. In contrast, the UD estimator for home range size was consistently similar to the one we observed when using all data points available for each individual, regardless of how many data points we used. Even when using only 5 data points, the home range sizes that we estimated were very similar to those we found when using 10 or more observations. The main impact that decreasing the sample size had on the home range size calculated with a UD estimate was a decrease in accuracy - the spread of estimates around the observed value was larger for smaller samples.

Conclusions: Consistent with past investigations that compared different estimation approaches of home range size (Socias-Martinez et al., 2023, cited in main text), we found that the MCP measure of home range size is highly sensitive to the number of repeated captures for each individual. However, estimating home range size using UD was not very sensitive to sample size and even sub-samples as small as 5 provided a reliable estimate of home range size.

Given this investigation we decided to only use the UD estimation of home range size in our study - to avoid biases in home range size that might result from differences in sample size across individuals. Furthermore, because a sub-sample of 5 data points provided a reliable estimate of home range size, that was similar to a home range size calculated with 10 or more points, we included in our analysis all animals that had 5 or more re-captures.

2. Mass of small and large *Peromyscus*

Figure S2: Small (*maniculatus*, *leucopus*) and large (*keeni*, *truei*, *gossypinus*, *attwateri*, and *boylii*) *Peromyscus* species had different mass (left). Body condition was calculated separately for big and small species because the relationship between mass and hindfoot length differed for big (middle) and small (right) species.



3. Model comparison for *Peromyscus*:

```
# no interaction terms:
m1=glmer(UD ~ sex + vegType + meanMNKA + latitude + bodyCondition +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

# models with interactions:
m2=glmer(UD ~ sex + vegType * latitude + meanMNKA + bodyCondition +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m3=glmer(UD ~ sex * bodyCondition + vegType + latitude + meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m4=glmer(UD ~ sex * bodyCondition + vegType * latitude + meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m5=glmer(UD ~ sex + bodyCondition * latitude + vegType  + meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m6=glmer(UD ~  bodyCondition + latitude + sex * vegType * meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m7=glmer(UD ~  bodyCondition + sex + latitude  * vegType * meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m8=glmer(UD ~  bodyCondition * sex + latitude * vegType * meanMNKA  +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m9=glmer(UD ~  bodyCondition * sex * meanMNKA + latitude * vegType   +
          (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m10=glmer(UD ~  vegType + sex + latitude * bodyCondition * meanMNKA  +
           (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m11=glmer(UD ~ sex * meanMNKA + latitude + bodyCondition +  vegType +
           (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))

m12=glmer(UD ~ sex * meanMNKA * bodyCondition + latitude  +  vegType +
           (1 | year) + (1 | site), data = ao_ranges, family = Gamma(link = "log"))
```

Table S1: Model comparison results for *Peromyscus* genus.

Name	Model	AIC (weights)	AICc (weights)	BIC (weights)	R2 (cond.)	R2 (marg.)	ICC	RMSE	Sigma
m8	**glmerMod**	**39424.2 (0.982)**	**39424.5 (0.982)**	**39528.4 (<.001)**	**0.212**	**0.168**	**0.053**	**1191.150**	**0.822**
m6	glmerMod	39446.2 (<.001)	39446.4 (<.001)	39544.6 (<.001)	0.217	0.162	0.066	1198.529	0.823
m3	glmerMod	39441.4 (<.001)	39441.5 (<.001)	39505.1 (0.851)	0.209	0.157	0.062	1197.356	0.828
m7	glmerMod	39432.5 (0.015)	39432.8 (0.016)	39531.0 (<.001)	0.210	0.167	0.052	1196.054	0.822
m12	glmerMod	39439.9 (<.001)	39440.0 (<.001)	39520.9 (<.001)	0.211	0.160	0.062	1196.564	0.824
m9	glmerMod	39437.7 (0.001)	39437.9 (0.001)	39530.4 (<.001)	0.206	0.157	0.058	1196.205	0.822
m4	glmerMod	39438.9 (<.001)	39439.1 (<.001)	39514.2 (0.009)	0.204	0.154	0.059	1197.234	0.825
m1	glmerMod	39450.9 (<.001)	39451.0 (<.001)	39508.8 (0.132)	0.206	0.154	0.061	1202.246	0.829
m11	glmerMod	39452.8 (<.001)	39452.9 (<.001)	39516.5 (0.003)	0.206	0.154	0.062	1202.353	0.829
m5	glmerMod	39452.9 (<.001)	39453.0 (<.001)	39516.6 (0.003)	0.206	0.154	0.061	1202.232	0.829
m2	glmerMod	39448.8 (<.001)	39448.9 (<.001)	39518.3 (0.001)	0.201	0.151	0.059	1202.463	0.827
m10	glmerMod	39449.5 (<.001)	39449.7 (<.001)	39530.6 (<.001)	0.201	0.158	0.051	1200.175	0.831

Figure S3: Relationship between animal density and latitude.

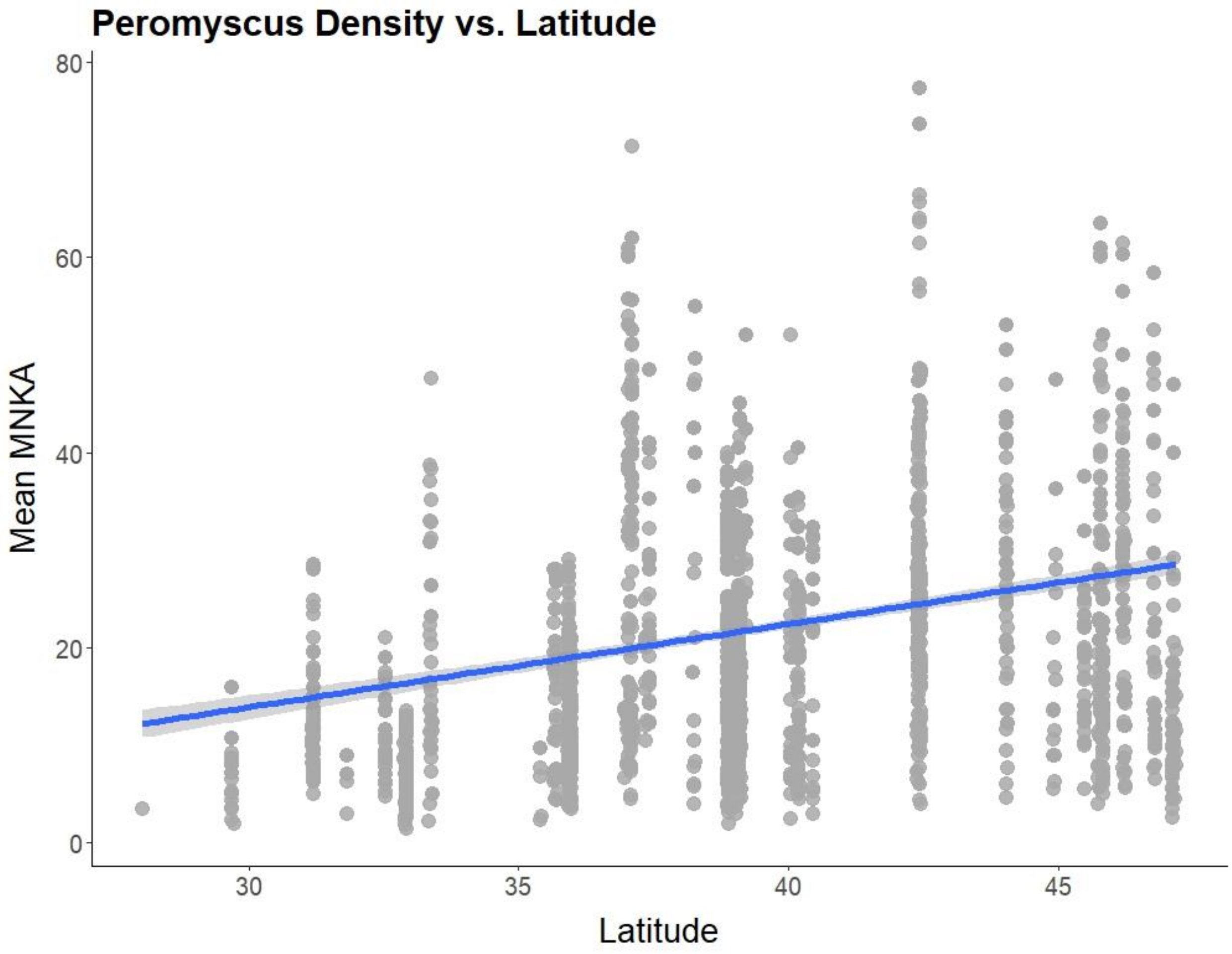
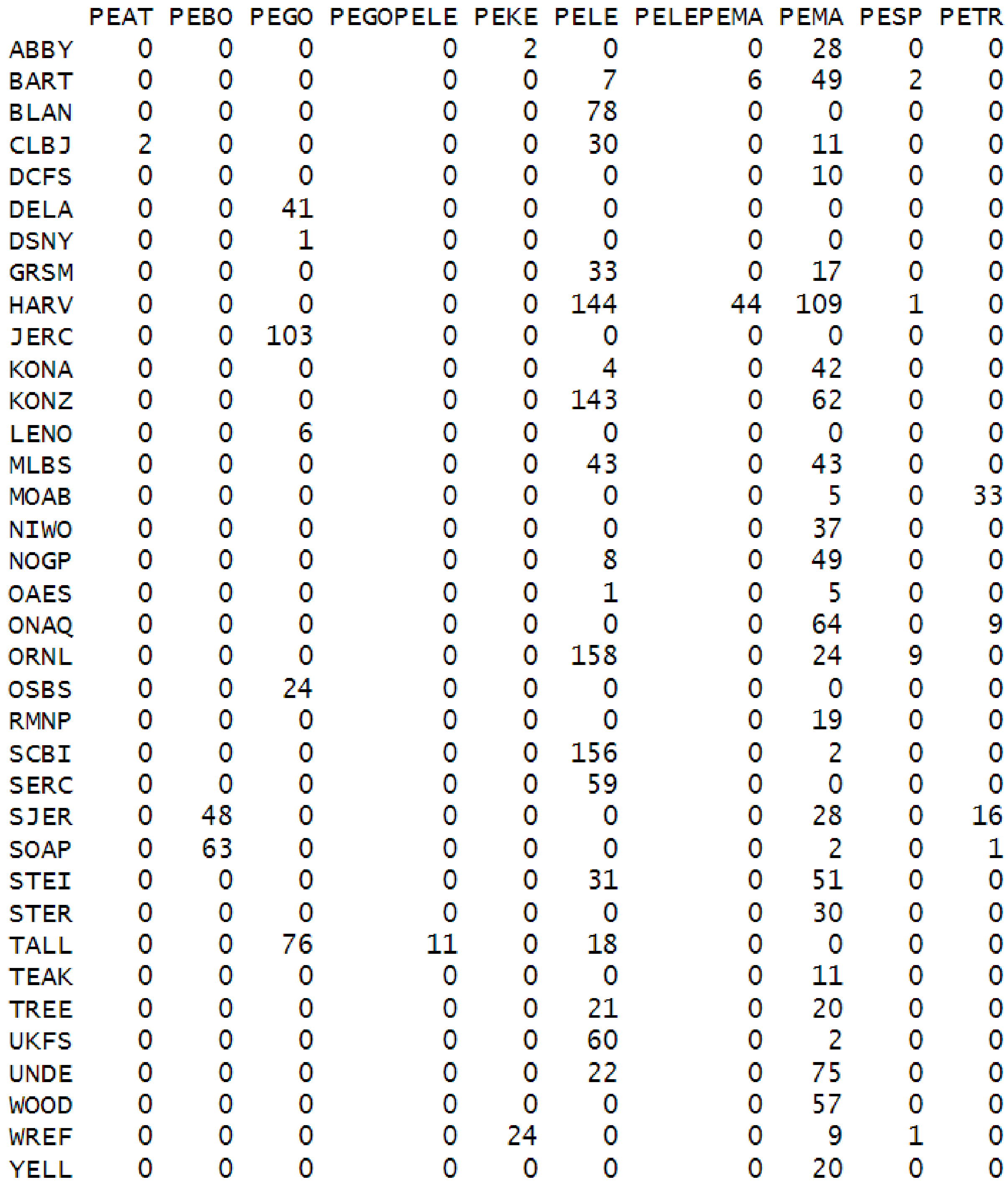


Table S2: Number of individuals from each *Peromyscus* species (columns) at each NEON site (rows) in our dataset. Note that the most abundant species (PEMA and PELE) occur at almost all NEON sites.



```
     PEAT PEBO PEGO PEGOPELE PEKE PELE PELEPEMA PEMA PESP PETR
ABBY    0    0    0        0    2    0        0   28    0    0
BART    0    0    0        0    0    7        6   49    2    0
BLAN    0    0    0        0    0   78        0    0    0    0
CLBJ    2    0    0        0    0   30        0   11    0    0
DCFS    0    0    0        0    0    0        0   10    0    0
DELA    0    0   41        0    0    0        0    0    0    0
DSNY    0    0    1        0    0    0        0    0    0    0
GRSM    0    0    0        0    0   33        0   17    0    0
HARV    0    0    0        0    0  144       44  109    1    0
JERC    0    0  103        0    0    0        0    0    0    0
KONA    0    0    0        0    0    4        0   42    0    0
KONZ    0    0    0        0    0  143        0   62    0    0
LENO    0    0    6        0    0    0        0    0    0    0
MLBS    0    0    0        0    0   43        0   43    0    0
MOAB    0    0    0        0    0    0        0    5    0   33
NIWO    0    0    0        0    0    0        0   37    0    0
NOGP    0    0    0        0    0    8        0   49    0    0
OAES    0    0    0        0    0    1        0    5    0    0
ONAQ    0    0    0        0    0    0        0   64    0    9
ORNL    0    0    0        0    0  158        0   24    9    0
OSBS    0    0   24        0    0    0        0    0    0    0
RMNP    0    0    0        0    0    0        0   19    0    0
SCBI    0    0    0        0    0  156        0    2    0    0
SERC    0    0    0        0    0   59        0    0    0    0
SJER    0   48    0        0    0    0        0   28    0   16
SOAP    0   63    0        0    0    0        0    2    0    1
STEI    0    0    0        0    0   31        0   51    0    0
STER    0    0    0        0    0    0        0   30    0    0
TALL    0    0   76       11    0   18        0    0    0    0
TEAK    0    0    0        0    0    0        0   11    0    0
TREE    0    0    0        0    0   21        0   20    0    0
UKFS    0    0    0        0    0   60        0    2    0    0
UNDE    0    0    0        0    0   22        0   75    0    0
WOOD    0    0    0        0    0    0        0   57    0    0
WREF    0    0    0        0   24    0        0    9    1    0
YELL    0    0    0        0    0    0        0   20    0    0
```